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BEHAVIOR OF LATERAL ROOTS IN WINTER WHEAT AS AFFECTED BY TEMPERATURE

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HUANG B.-R., TAYLOR H. M. and MCMICHAEL B. L. *Behavior of lateral roots in winter wheat as affected by temperature.* ENVIRONMENTAL AND EXPERIMENTAL BOTANY **31,** 187–192, 1991.—The experiment was conducted to evaluate the effects of temperature on growth of laterals on the seminal roots of wheat (*Triticum aestivum* L.). Wheat seedling root growth was measured on alternate days for 28 days beginning at 4 days after planting. The length, number, time of emergence, and the distance apart of primary lateral roots and the length of the unbranched axis were determined on the plants under air temperatures of 10, 20, 25 and 30°C. The primary lateral roots (i) emerged earlier with increased temperature, and developed closer to the tip of the seminal axis at 20 and 30°C than at 10 and 25°C, (ii) were more closely spaced along the seminal axis at the higher temperatures, (iii) increased in density along a segment of root within a period of time after planting that varied with temperature, indicating that lateral root emergence did not follow an acropetal sequence, (iv) had a distribution in length that was unaffected by temperature, (v) were fewest in number and least in length at 10°C, greatest in number and length at 25°C, and were intermediate in length and number at 20 and 30°C, and (vi) had lengths that accounted for about 46, 83, 85 and 72% of the total seminal root length at 10, 20, 25 and 30°C, respectively.

INTRODUCTION

A major function of the root system is the absorption of water and nutrients from the surrounding medium. Lateral roots play an important role in this function by (i) increasing greatly the total length and surface area of the actively absorbing root system thereby increasing the volume of soil being exploited for water and nutrients, and (ii) transporting a high proportion of absorbed water and salts to the shoot.[2] The development of lateral roots is known to differ greatly with variety and with environmental factors. HACKETT[7] and DREW *et al.*[4] showed that local application of nitrates stimulated lateral root initiation and growth in a nitrogen limited situation. WIERSUM,[17] HACKETT[7] and MAY *et al.*[13] claimed that nutrient deficiency and nutrient concentration influenced root-branching patterns. STONE and TAYLOR,[15] GREGORY,[5,6] and BOWEN and ROVIRA[2] reported that temperature had a dramatic effect on production and growth of laterals in soybean, pearl millet and wheat, respectively. Growth and production of lateral roots were greatly reduced at lower temperatures. DADAY and WILLIAMS[3] observed that high temperature restricted the formation of lateral roots in lucerne.

Although these studies have established that growth and morphology of roots are influenced

markedly by different environmental factors, quantitative information on these effects is scarce. In particular, there is little information about temperature effect on the timing of lateral root initiation, and on distribution pattern, density and growth rate of lateral roots in winter wheat, which are important plant factors influencing water and nutrient uptake. Moreover, the usefulness of root models is limited by (i) inadequate description of root morphology (especially branching pattern)[12] and (ii) inability to incorporate known effects of plant age, temperature and other factors that affect root growth, into quantitative equations. Quantitative information of this nature would be a useful tool in plant selection, in understanding crop and soil management practices, and in root growth modeling.

The objectives of this study were to: (i) evaluate the effect of air temperature on the morphology of lateral roots in winter wheat, and (ii) provide quantitative information on root dynamics for use in wheat root stimulation models.

MATERIALS AND METHODS

The experiment was carried out in a controlled environmental growth chamber at Texas Tech University. Winter wheat (*Triticum aestivum* L., cv. Newton) was grown in polyvinylchloride tubes at four constant air temperatures of 10, 20, 25 and 30°C with a 12-hr photoperiod controlled by fluorescent lights (intensity 780 $\mu E/m^2 \cdot sec$). Temperature was monitored by a hygrothermograph. Tubes (5 cm diameter by 80 cm long), with a nylon screen taped over the bottom, were filled with air-dry, sterilized, coarse sand. Three seeds were sown in each tube and thinned to one plant after the seedlings had emerged. Plants were watered with 100 ml half-strength Hoagland's solution[10] once each day.

Three plants from each temperature of 10, 20, 25 and 30°C were randomly harvested on alternate days beginning at 4 days after planting (DAP). At 10, 20 and 30°C, the harvests were concluded at 28 DAP but at 25°C, the last plants were harvested at 24 DAP since the roots had reached the bottom of the tubes. All tubes required for measurement at a particular temperature were grown in the growth chamber at one time. The procedure was then repeated at a different temperature in the same growth chamber.

At harvest, the roots were washed from the sand. Number, length and position of all primary lateral roots on all seminal axes were determined manually. From these measurements, the distribution in length of laterals along the primary seminal root axis (the relationship between the lengths of laterals and the distances from the base of the axis of their points of origin) and length of the unbranched axes (distance from the most distal primary lateral 1 mm long to the axis tip) were determined on each seminal axis for each of the three plants from each treatment. The number of primary lateral roots that had emerged were counted in successive 1 cm zones from the basal end of the primary seminal root axis in order to obtain lateral density. Days after planting when primary laterals were first observed on the three plants (i.e. a 1 mm length of lateral was visible) were recorded. Thermal time required for root emergence was calculated in degree days (°C day), using zero Celsius as the base temperature. Thermal time is defined as $\theta = (T - T_b)t$, where θ is the thermal time (°C day), T_b is the base temperature (°C), T is the prevailing temperature (°C), and t is the time (day).

Root pieces, 5 mm long, were cut off at different distances from the root tips of the primary seminal axes, embedded in paraffin, sectioned longitudinally and examined under a light microscope to determine existence of any undeveloped lateral root primordia.

The experiment design was considered to be a series of experiments repeated over temperatures (i.e. an experiment involved a specific temperature) with three plants per datum nested within temperatures as described by KEMPTHORNE.[11] Temperatures were the main plots, and times of sampling were subplots. Tubes designated for a particular time were completely randomized within each temperature. Differences between the treatments in terms of length of unbranched seminal axes, density, total length and number of primary laterals were determined by analysis of variance. The distribution of the lateral roots along seminal axes was evaluated by regression analysis.

HACKETT's[8] terminology was adopted to describe the lateral roots.

Table 1. The effect of growing condition temperature on the average seminal root length (cm) at various days after planting (DAP)

	Growth temperature (°C)			
DAP	10	20	25	30
4	0.3b*	1.7b	4.7a	4.3a
6	1.8b	3.4b	7.5a	6.3a
8	2.0c	5.6b	11.4a	6.7b
10	2.7c	8.4b	16.7a	6.8bc
12	6.3c	8.8bc	17.1a	13.4ab
14	8.2c	12.4bc	30.0a	18.0b
16	9.8c	15.4bc	41.4a	18.3b
18	10.3c	18.3bc	43.2a	27.0b
20	13.7c	19.3bc	51.6a	29.5b
22	19.6c	23.9bc	57.6a	36.2b
24	20.1c	26.7c	67.8a	47.6b
26	28.3c	29.2c	—	48.7b
28	29.8c	35.4bc	—	53.8b

* Means within rows followed by the same letter are not significantly different.

RESULTS

Seminal axes lengths

By 8 days after planting (DAP) average lengths of the seminal axes were greater at 25°C than at 10, 20 or 30°C (Table 1). At most of the sampling times, lengths at 30°C were greater than those at 10°C but often there was no difference in length between the 20 and 30°C plants.

Length of unbranched seminal axes

At 12–20 DAP, lengths of the unbranched portions of the seminal root axes were greater at 25°C than at 20 or 30°C but at 16 or 20 DAP the unbranched portion of the seminal axes grown at 10°C was not different from that at 25°C (Table 2). Length of the unbranched portion did not vary with time between 12 and 20 DAP at 10 and 20°C but did vary with time at 25 and 30°C. BOWEN[1] observed that the unbranched portion of *Pinus radiata* roots decreased with temperature.

Time of primary lateral root emergence

Air temperature had a significant effect on the time at which lateral roots first emerged from the seminal axes. Emergence commenced in 4 days at 25°C, in 5 days at 30°C, in 7 days at 20°C but required 14 days at 10°C. The thermal times were 140, 140, 100 and 150 degree days at 10, 20, 25 and 30°C, respectively.

Table 2. Effect of temperature on the length of unbranched seminal axes

	Temperature (°C)			
DAP	10	20	25	30
12	8.4aB	6.8aB	11.4bA	6.8bB
16	11.9aA	6.7aB	16.4aA	8.5bB
20	13.4aA	6.9aB	13.6baA	8.8aB

Means within the same column followed by the same lowercase letter are not significantly different at the 0.05 level. Means within the same row followed by the same uppercase letter are not significantly different at the 0.05 level based on a LSD test.

Density of primary lateral roots along seminal axes

After 12 days following planting, there was a greater spacing between primary lateral roots on axes grown at 10°C than at 30°C. The density of primary laterals was intermediate at 20 and 25°C (Fig. 1). There is no significant ($P < 0.05$) difference between the density of lateral roots at 20 and 25°C. During the initial growth (up to 12 DAP), however, the density of primary lateral roots was significantly higher at 25°C than at 10 and 20°C, but not significantly different from that of 30°C.

The relationship between the density of pri-

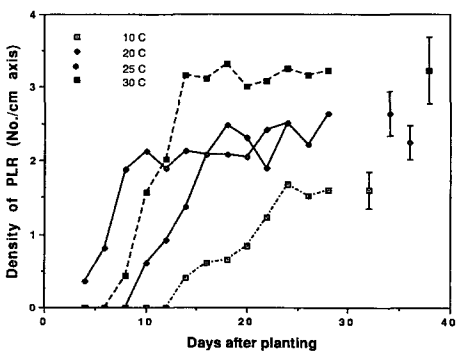

FIG. 1. Change in density of primary lateral roots (PLR) on the root axis with time at the different temperatures. Vertical bars indicate LSD (0.05) for comparison of density at different times.

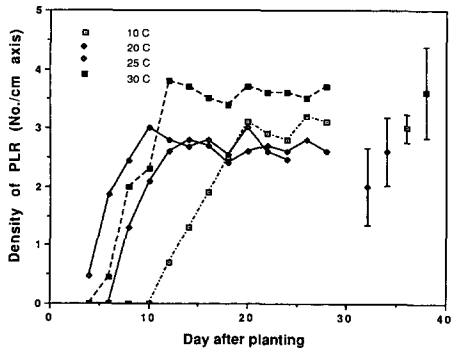

FIG. 2. Change in density of primary lateral roots (PLR) over a 5 cm region near the base of the seminal root axis. Vertical bars indicate LSD (0.05) for comparison of density at different times.

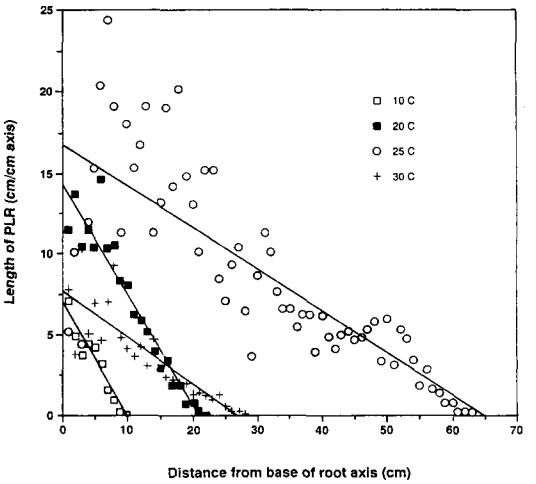

FIG. 3. Effect of temperature on the distribution in length of primary lateral roots (PLR) along the root axis at 20 days after planting.

mary lateral roots and time after planting consists of two phases (Fig. 1). First, a significant increase ($P < 0.05$) in the density of lateral roots occurred during the first 24, 18, 10 and 14 days after planting at 10, 20, 25 and 30°C, respectively. This period was followed by a phase in which no increase in density occurred with time. This trend was similar for all four temperatures, indicating that the time required for all primary lateral roots to develop on a seminal axis is temperature dependent. A count of the primary lateral roots over a 5 cm region near the base of seminal axes (Fig. 2) shows that their density increased at the basal portion until 20, 14, 10 and 12 days after planting at 10, 20, 25 and 30°C, respectively. This result means that some new lateral roots must be formed among pre-existing ones.

Distribution pattern of primary lateral roots along seminal axes

The distributions of length of primary lateral roots on each centimeter of the primary seminal axis from each of the three plants were examined at 16, 18 and 20 days. The longest laterals tended to occur near the base of the seminal axes for all four temperatures (Fig. 3) and data from the different days showed a similar trend. The rate at which length decreased with distance from the basal end of the seminal axis was significantly ($P < 0.05$) greater for 10°C ($y = 7.00 - 0.72x$, $r^2 = 0.922$) and 20°C ($y = 14.35 - 0.69x$, $r^2 = 0.919$) than at 25°C ($y = 16.85 - 0.26x$, $r^2 = 0.652$) and 30°C ($y = 7.72 - 0.29x$, $r^2 = 0.755$). The rate was not significantly different between 10 and 20°C, and between 25 and 30°C.

The length of individual primary lateral roots along the seminal axes changed with temperature, with the length being the greatest at 25°C and least at 10°C. The individual lateral root lengths were greater at 20°C than that at 30°C through most of the distances from the base of the root axis.

Production and growth of lateral roots

Temperature exerted a dramatic effect on production and growth of lateral roots. The number of primary laterals increased from 10 to 25°C, and decreased as the temperature increased to 30°C (Fig. 4). Total numbers of lateral roots seemed to be greater at 30°C than that at 20°C, but they were not significantly ($P < 0.05$) different. Lateral root formation was greatly restricted at 10°C. The total length of primary lateral roots was much greater ($P < 0.05$) at 25°C than at 10, 20 and 30°C (Fig. 5). There was no significant difference ($P < 0.05$) between 20 and 30°C for total lateral root length. However, the individual roots were longer at 20°C. The growth of lateral roots was low at 10°C due to a marked decrease

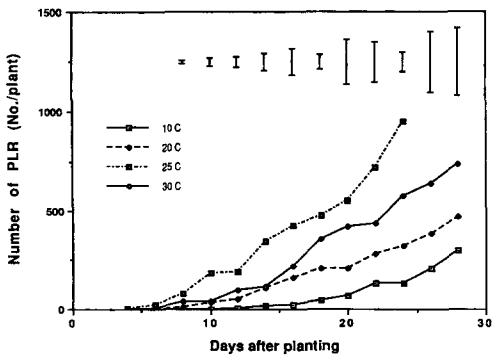

FIG. 4. Effect of temperature on the number of primary lateral roots (PLR). Vertical bars indicate LSD (0.05) for treatment comparisons at a specific time.

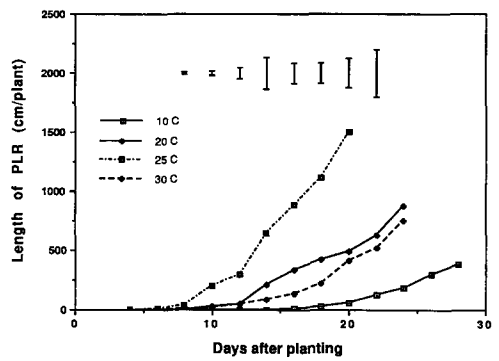

FIG. 5. Effect of temperature on the total length of primary lateral roots (PLR). Vertical bars indicate LSD (0.05) for treatment comparisons at a specific time.

both in the number and lengths of lateral roots. These results are similar to those of BOWEN.[1] The greater total length of lateral roots at 20, 25 and 30°C was due to greater number and length of laterals at 25°C, to more laterals at 30°C, and to longer laterals at 20°C. Both the number and length of primary lateral roots changed with temperature, and increased almost exponentially with time as axes produced primary laterals. This result agrees with the observations by GREGORY[6] for pearl millet.

At 20 days after planting, primary lateral root length accounted for about 83 and 85% of the total seminal root length at 20 and 25°C, respectively (Table 3). The proportion of the primary laterals at 30°C was significantly ($P < 0.05$) less than the proportion of primary laterals at 20 or 25°C, but much greater than that at 10°C.

Table 3. Proportion of primary lateral roots to the whole seminal root system as influenced by temperature at 20 days after planting

Temperature (°C)	Length of SR axes (cm/plant)	PLR length (cm/plant)	Percentage of PLR to SRL (%)
10	73.0	62.5	46.1C*
20	97.6	463.0	82.7A
25	274.8	1535.8	84.8A
30	138.0	352.3	71.8B

LSD ($P < 0.05$).
Plant age, 20 days after planting.
* Means with the same letter are not significantly different.
SRL, Total seminal root length.
PLR, Primary lateral root.

DISCUSSION AND CONCLUSIONS

Temperature had a marked impact on growth and morphology of the seminal root system of wheat. Among the four temperatures studied, a temperature of 25°C seemed to be the most desirable for wheat root growth and extensive exploration of the soil volume.

Elongation rate of the seminal root axes was greatest at 25°C and was least at 10°C. The distance from the tip at which lateral roots first emerged was greatest at 25 and 10°C and usually was significantly less at 20 and 30°C.

The total length and number of primary laterals on the seminal axes increased with temperature to 25°C. There was also a lower rate of change in lateral roots with distance on the seminal axis at 25 and 30°C than at 20 and 30°C.

In general, lateral primordia developed in an acropetal sequence along parent roots.[14] HACKETT and ROSE[9] mentioned that first order laterals of barley did not follow an acropetal sequence. In the region where first order laterals were emerging, the distal one of an adjacent pair of roots often emerged before the proximal one. In our experiment, the density of lateral roots increased

for a period of time near the base of the seminal roots, indicating that lateral root primordium inception occurred and hence some new lateral roots emerged between the existing laterals. Microscopic examination of longitudinal sections of seminal axes showed that there were some primordia of laterals still within the epidermis of the parent axis near its base. The existence of small primordia in more proximal parts of the seminal axes occurs because they develop at a slower rate than other primordia.[16] These results indicate that primordium initiation and primary lateral root emergence do not strictly follow an acropetal sequence in wheat.

Overall, our results indicate that the seminal roots of the wheat cultivar that we used will root into a greater volume of soil and will explore more of the rooted volume at 25°C than at lower or higher temperatures. Thus plants grown at 25°C will usually obtain access to greater quantities of water and nutrients than those grown at 10, 20, or 30°C.

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